

# New findings of *Prototherium ausetanum* (Mammalia, Pan-Sirenia) from paving stones in Girona (Catalonia, Spain)?

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## Abstract

Taxonomic and morphological approaches on Eocene sirenians from Catalonia (Spain) benefit from a newly discovered specimen found in a quite unusual locality, the pedestrian zone in the city of Girona. Two fossil-bearing limestone slabs from middle Eocene (Bartonian) layers of a quarry in the wider surrounding area north-west of Barcelona, were CT-scanned in the Clínica Girona to enhance more detailed investigations. Post-processing of the scans and, as far as possible, 3D-reconstruction of the preserved elements in the slabs was performed at Museum für Naturkunde Berlin. Thereby, a skull of a *Dugong* specimen was used as a reference point. Based on the combined analysis of macroscopic and CT-data, the specimen most likely represents *Prototherium ausetanum* Balaguer & Alba, 2016 and complements the available information of the holotype and hitherto only known specimen of that species. The Girona specimen is an adult, but small individual that corroborates *P. ausetanum* as a generally small-sized species compared to other known *Prototherium* taxa.

## Key Words

3D-visualisation, CT-scanning, Eocene, morphology, taxonomy, urban fossil

## Introduction

In a preceding study (Voss et al. 2019), one of the oldest sirenian remains in Europe found under peculiar circumstances was introduced to the scientific community and the wider audience of citizen scientists and the general public interested in geological heritage and geotourism.

Two limestone slabs from the late middle Eocene of Sant Vicenç de Castellet (Catalonia, NE Spain, Fig. 1) were once processed in a pedestrian pavement in the city of Girona and were recently detected to contain remains of an extinct sirenian, a large, herbivorous marine mammal. Based on macroscopic investigations and first CT-data, the fossil find could be confirmed as belonging to a single specimen (Voss et al. 2019). As such, it is a particularly lucky circumstance that the two fossil-bearing slabs have

been placed precisely next to each other. Furthermore, Voss et al. (2019) could limit the relative age of the specimen and its taxonomic identity. Mainly judging from the dental formula, this sea cow material represents a young adult belonging to the genus *Prototherium*.

The objective of this follow-up article is to verify the preliminary results from Voss et al. (2019) by resolving other still outstanding issues. The latter refers especially to the taxonomic assignment on the species level. For the time being, the Girona sea cow is tentatively assigned to *P. ausetanum* considering the palaeobiogeographic and stratigraphic background. If this can be confirmed, this specimen would complement the available information of the holotype, and hitherto only known specimen, of *P. ausetanum* described by Balaguer and Alba (2016). Based on CT-data and subsequent 3D-reconstruction of



**Figure 1.** Panoramic view of the SW side of the limestone quarry southeast of Sant Vicenç de Castellet showing the massive blocks of Bartonian carbonates bound by micritic matrix, and containing besides macroforaminifers, such as nummulites and discoeyclids, bryozoans, corals, and bivalves vertebrate remains (here described: MAC GIR-042375).

the preserved sea cow remains, the identification of additional diagnostic features referring to the snout region, the dentition, and the basicranium is uncovered. As a consequence, this allows a more accurate morphological and taxonomic interpretation of the Girona specimen. In light of the wider picture, this study will help to better understand the evolutionary history and diversity especially of Eocene sirenians.

## Material and methods

For this subsequent and complementing article on fossil remains of a sea cow found in two slabs in the pedestrian zone in the city of Girona, CT-scans made at the Clínica Girona were analyzed in detail as best as possible. The CT used here was a GE light speed Optima CT520 (General Electric Company, GE Healthcare, Chalfont St Giles/UK) and was utilized under the following protocol parameters: slice thickness 0.625 mm; space 0.31 mm; pitch 0.56 mm; single collimation width 0.625 mm; pixel spacing  $0.4 \times 0.4$ ; matrix  $512 \times 512$ ; field of view 250 mm; convolution kernel: Boneplus; tube voltage and stabilizer 120 kVp, 140 mA. Post-processing of the scanned slabs, i.e., segmentation of the individual bones and the combination of the separate section planes in 3D, is hampered by inclusions of iron-rich minerals and by the characteristic

thick and dense sirenian bones itself keeping the contrast between bone and surrounding limestone relatively low. Nevertheless, the individual bones could be segmented and combined in 3D allowing further morphological examination of the skull. Analysis and visualization of the CT-data were performed with VGStudio MAX 2.2.

The taxonomic-morphological comparisons of the Girona specimen MAC GIR-042375 are based almost solely on personal investigations of the taxa for comparison. This refers to *P. veronense* De Zigno, 1875 and *P. intermedium* Bizzotto, 1983 from the Bartonian and Priabonian of North Italy, respectively, stored at MGPD (MV). In each case, the holotype and associated specimens were investigated as is provided by Voss (2013: appendix 2). One of the results of Voss' (2013) study is a phylogeny of Sirenia based on a revised character-taxon matrix. This implies that the character coding of all considered sirenian taxa, including *P. veronense* and *P. intermedium*, was verified and, if necessary due to personal observations, adjusted. Morphological characters that are relevant here and scored contrary to other studies (e.g., Domning 1994; Díaz-Berenguer et al. 2018, 2022) are also stressed in the comparative Description chapter. Moreover, the holotypes, and hitherto only known specimens, of *P. montserratense* and *P. solei* Pilleri et al., 1989 were personally examined at MGSB (MV, OH). The holotype MGSB 44892 of *P. montserratense* from Castellbell i el Vilar (Catalonia, Spain) is

embedded in the surrounding sediment, but still reveals a number of cranial and postcranial elements that represent “probably a complete animal” (Pilleri et al. 1989: 37). Reference to selected material is provided in the chapters Description and Discussion when relevant for comparison. The holotype MGSB 48657 of *P. solei* from Tona (Catalonia, Spain) represents a partially preserved specimen. Thereof, the following elements were investigated: a skullcap including the frontal, parietal, supraoccipital, and the left zygomatic process of the squamosal (MGSB 48657-1), the left mandibular ramus with  $M_{1-3}$  (MGSB 48657-2), a premaxillary fragment (MGSB 48657-3), the partially preserved maxilla with molars (MGSB 48657-4), and the left humerus (MGSB 48657-8). Comparisons with *Prototherium ausetanum* are based on the morphological descriptions from Balaguer and Alba (2016).

### Institutional abbreviations

**MAC**, Museu d’Arqueologia de Catalunya, Girona, Spain; **MGPD**, Museo di Geologia e Paleontologia, Padova, Italy; **MGSB**, Museu Geològic del Seminari de Barcelona, Spain; **RGHP**, Réserve géologique de haute Provence, Digne-les-Bains, France; **ZMB**, Museum für Naturkunde Berlin, Zoological Collection, Germany

### Systematic palaeontology

**Class Mammalia Linnaeus, 1758**

**Afrotheria Stanhope et al., 1998**

**Tethytheria McKenna, 1975**

**Pan-Sirenia O’Leary et al., 2013**

**Genus *Prototherium* de Zigno, 1887**

***Prototherium cf. ausetanum* Balaguer & Alba, 2016**

**Nomenclatural remark.** The present systematic palaeontology considers the quite recently established clade Pan-Sirenia, O’Leary et al., 2013. Thereby, O’Leary et al. (2013: supplementary material, table 4) apply the total group concept (Jefferies 1979) and distinguish between Pan-Sirenia as representing the total clade of Sirenia Illiger, 1811, whereas Sirenia is redefined and restricted to the node-based crown group as the least inclusive clade containing all living sirenians, their last common ancestor, and all of its descendants. The same concept is introduced later again by Vélez-Juarbe and Wood (2018). Therefore, priority, and hence reference for Pan-Sirenia, is given here to O’Leary et al. (2013).

**Material.** MAC GIR-042375, partial skull and rib remains documented in urban paving stones of Girona, Catalonia, Spain.

**Locality.** Limestone quarry south of Sant Vicenç de Castellet, central Catalonia, Spain.

**Stratigraphic position.** Late Bartonian, middle Eocene. The age of the find is corrected from early

Bartonian (Voss et al. 2019) to late Bartonian (Galindo et al. 2003).

### Description

The sirenian remains are embedded in a shallow carbonate platform sediment consisting of an alternation of biomicritic limestones, lutites and bluish-grey claystones (Figs 1, 2), and are distributed on two slabs, each measuring 2 cm in thickness. The preserved elements mainly belong to the skull of a single specimen and include parts of the rostrum (premaxilla and maxilla), frontal, vomer, basi-cranium, and fragments of the zygomatic arch (jugal and squamosal). From the teeth, the upper molars  $M^1$ - $M^3$  including crowns and roots are preserved. Otherwise, the dentition is indicated by the presence of alveoli. In addition to the macroscopic analysis, CT-scanning and post-processing allow more detailed morphological examination of the preserved skull parts. As already performed in Voss et al. (2019), the slab preserving a relative upper region of the skull roof and snout is designated as slab 1, the other representing a relatively deeper level within the skull is designated as slab 2 (Fig. 3).

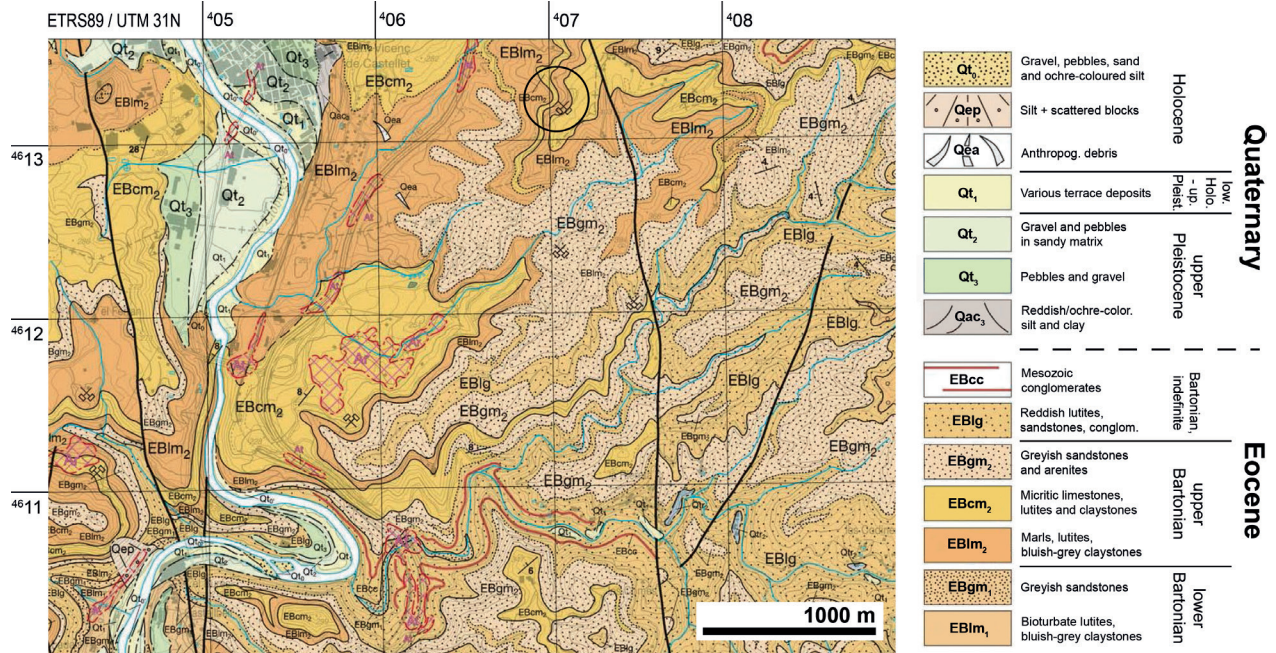
The first new observation refers to the orientation of the single fossil-bearing slabs. With the help of an adult skull of the extant dugong (*Dugong dugon*, ZMB\_MAM 69306), the partial skull was aligned in an anatomically correct position mainly considering the slope of both, the jugal and the rostrum. As a result, each slab shows oblique angles in the transversal plane, hence do not lie one-to-one at that specific level. For slab 1, the angles are 28.22° in lateral view, and 4.3° in frontal view; for slab 2, the angles are 28.22° in lateral view, and 6.0° in frontal view, respectively (Fig. 3a, b). This explains, amongst others, why each slab preserves skull elements from a vertically higher level on the right side and from a somewhat lower level on the left side. The same applies to the antero-posterior orientation of the slabs, which accordingly show skull elements from a lower level anteriorly and cranial parts from a higher level posteriorly. As it will be outlined below, the oblique orientation sometimes impedes the correlation of specific structures between the slabs, which resulted in amendments as to some observations made in Voss et al. (2019).

The distance between both slabs could be ascertained to be 11.4 mm (Fig. 3). As such, a total of 50 mm, i.e., 40 mm fossil-bearing stone plus circa 10 mm non-preserved interspace, is the basis for this study. This equals about 50% to 77% of the height of a typical Eocene-Oligocene sirenian skull (Voss 2013: appendix 3, Measurements of crania: top of supraoccipital to ventral sides of occipital condyles (de)).

Furthermore, the preliminary results by Voss et al. (2019) on the individual age and the taxonomic assignment of the Girona find can be verified.

Voss et al. (2019) determine the Girona specimen as representing at least a young adult based on the advanced





**Figure 2.** Modified extract from the geological map (Mapa geològic de Catalunya 1:25 000, Monistrol de Montserrat 392-1-1 (71-29)) showing the position of the limestone quarry (circle: SE Sant Vicenç de Castellet, E of Llobregat river) from which the pavement slabs containing the MAC GIR-042375 *Protherium* cf. *ausetanum* remains came from. All sediments from this area are dated to the late Bartonian.

state of wear of the M<sup>3</sup> and its position at the level of the posterior margin of the zygomatic orbital bridge (Mitchell 1973). At this point, an amendment to the preceding description in Voss et al. (2019) is necessary. While the position of the M<sup>3</sup> is confirmed in macroscopic view and in the CT-scans (Voss et al. 2019: fig. 6b, c), the position of M<sup>1-2</sup> as shown in slab 1 (Voss et al. 2019: fig. 6a) has to be adjusted. The two visible alveoli in the latter figure belong most certainly to P<sup>4</sup>-P<sup>3</sup> considering the higher anatomical level of slab 1 combined with the transversally non-planar cut of the slabs (Fig. 4a).

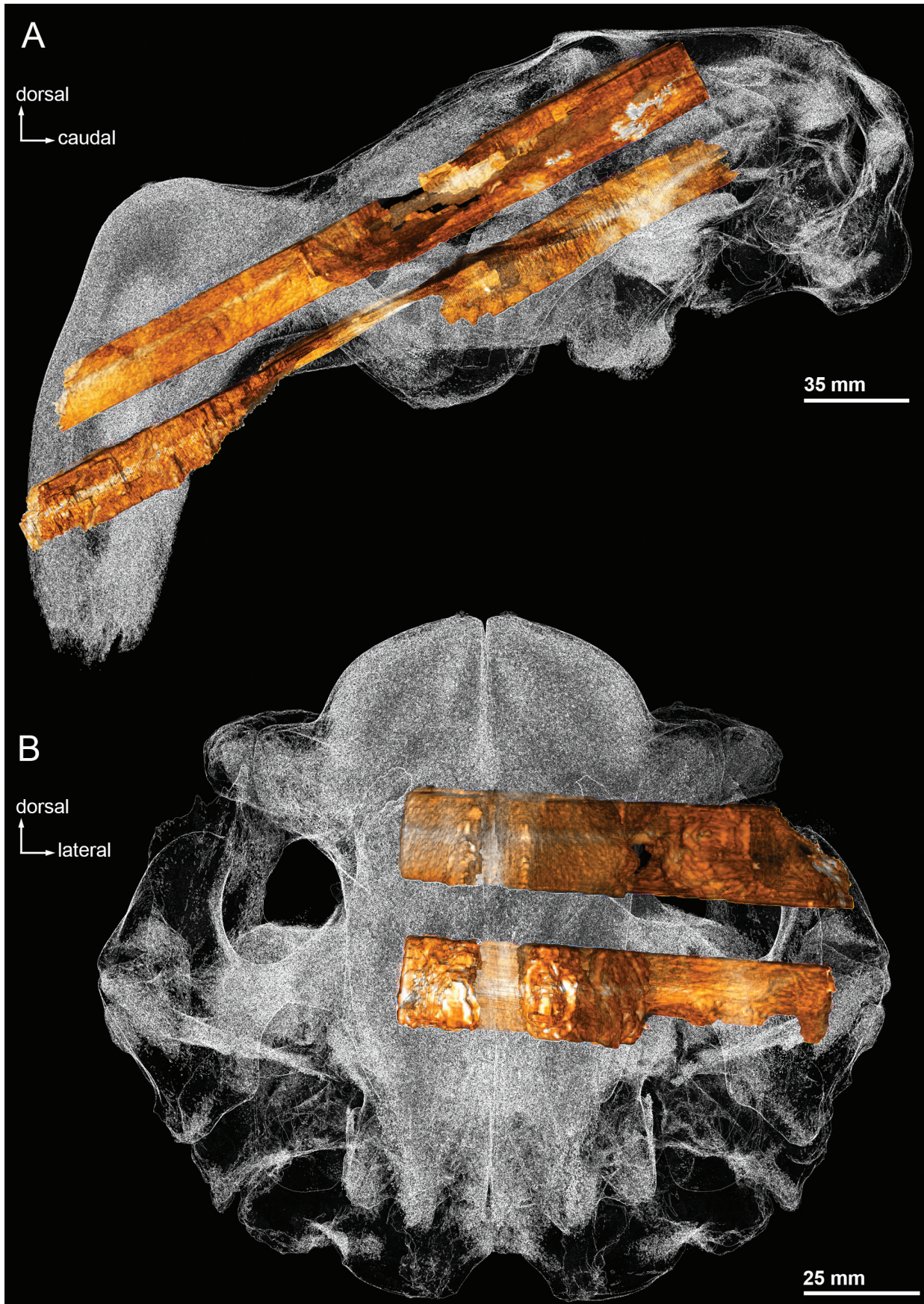
For relative age determination, it is also highly indicative whether sutures between certain bones are open, fused or even obliterated (Pocock 1940; Mitchell 1973). The contact between the basisphenoid and basioccipital is especially important for the identification of adulthood. Elements of the basicranium are clearly and best visible on the unpolished bottom side of slab 1 (Fig. 4a) showing parts of the basisphenoid, the spheno-occipital eminences, and the basioccipital that is mainly preserved with its left extension. The anterior ends of the spheno-occipital eminences mark the approximate contact between basisphenoid and basioccipital. Both bones are considered as being firmly fused, since there is no indication of a suture. This is also confirmed in the respective CT-Scan (Fig. 4b) despite interferences that reduce the scan quality. Consequently, the Girona specimen definitively belongs to an adult individual.

With respect to the taxonomic assignment, Voss et al. (2019) identified the Girona sea cow as a representative of the Eocene genus *Protherium* (and finally *P. ausetanum*) based on the antemolar dental formula.

This is corroborated also in this study and observable in slab 2 (Fig. 5). Thereby, Fig. 4a reflects mainly alveoli in macroscopic dorsal view of slab 2 and Fig. 4b shows the corresponding CT-scan with teeth in ventral view of slab 2. As a result, four alveoli for single-rooted premolars (P<sup>1-4</sup>) can be unambiguously ascertained (Fig. 5a). The complete number of premolars reflects plesiomorphic conditions and is characteristic for Eocene sirenians (e.g., Voss 2013). The most important feature is the absence of a persistent DP<sup>5</sup>, a molariform upper deciduous fifth premolar, which is a peculiarity in the dental formula of *Protherium* (e.g., Domning 1994; Bizzotto 2005; Balaguer and Alba 2016). While also the lack of DP<sup>5</sup> can be deduced directly from the preserved maxillary parts on the slabs, the presence and absence of alveoli is hardly observable in the corresponding CT-Scan even after careful post-processing and evaluation of the ventral side of the slab (Fig. 5b). This is primarily based on the fact that the contrast between sirenian bone and surrounding matrix is relatively low. Additionally, inclusions of iron-rich minerals cause harmful interferences.

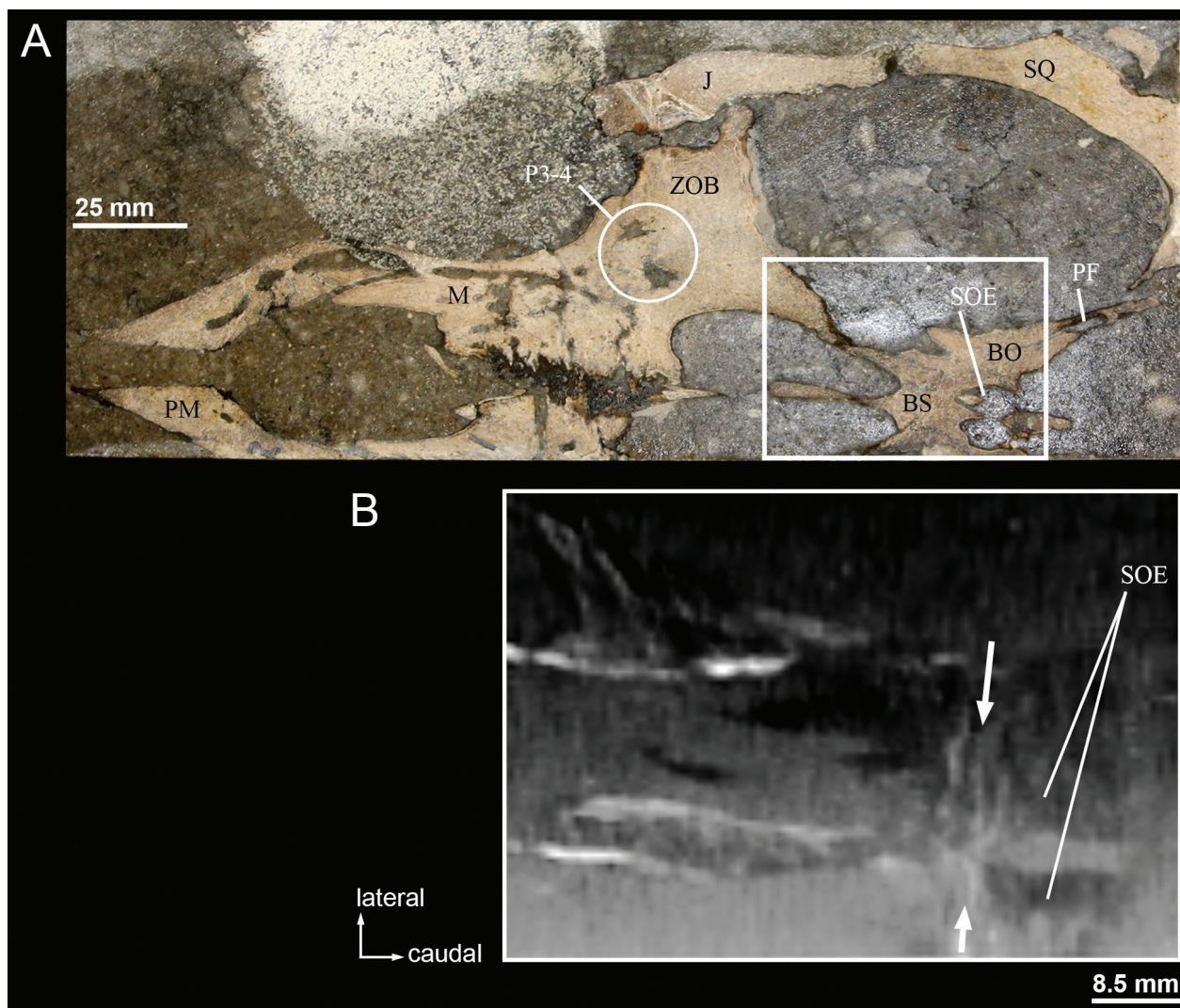
Nevertheless, the present results support the Girona specimen as belonging to the genus *Protherium*. As such, its identification on the species level focusses on comparisons with three *Protherium* species generally considered valid: *P. veronense* De Zigno, 1875 from the late middle Eocene (Bartonian) of Verona (Italy), *P. intermedium* Bizzotto, 1983 from the late Eocene (Priabonian) of Possagno (north-east from Verona, Italy), and the recently established *P. ausetanum* Balaguer & Alba, 2016 from the Bartonian of Tona (Catalonia, Spain). Additionally, the taxonomic-morphological comparisons are complemented by two further





**Figure 3.** Spatial orientation of the fossil-bearing slabs in **A.** Lateral view; **B.** Frontal view. CT-scans of the upper slab 1 and the lower slab 2 (both in color) are aligned in an anatomically correct position using the extant dugong as reference (grey-scaled CT-scan of *Dugong dugon* ZMB\_MAM 69306).





**Figure 4.** *Protheroherium* cf. *ausetanum*, MAC GIR-042375. **A.** Photograph; **B.** Corresponding CT-scan of slab 1 with focus on the basicranium. The unpolished bottom side of slab 1 (**A**) shows parts of the basisphenoid, the spheno-occipital eminences, and the basioccipital, all of which being firmly fused indicating adulthood. The CT-Scan of the basicranium (**B**) shows interferences, however, the suture between basisphenoid and basioccipital is unequivocally obliterated and estimated to be more or less level with the vertical interference (indicated by arrows). Abbreviations: BO, basioccipital; BS, basisphenoid; J, jugal; M, maxilla; PF, pharyngeal fossa; PM, premaxilla; P<sup>3-4</sup>, third and fourth upper permanent premolars; SOE, spheno-occipital eminences; ZOB, zygomatic-orbital bridge of maxilla.

*Protheroherium* species from the Bartonian of Catalonia, *P. solei* Pilleri et al., 1989 and *P. montserratense* Pilleri et al., 1989. As it will be discussed later, their status and affinities are uncertain (e.g., Domning 1996; Bizzotto 2005; Balaguer and Alba 2016). However, the geographic and stratigraphic occurrence of both species raise particular relevance for the comparison with specimen MAC GIR-042375 from Girona.

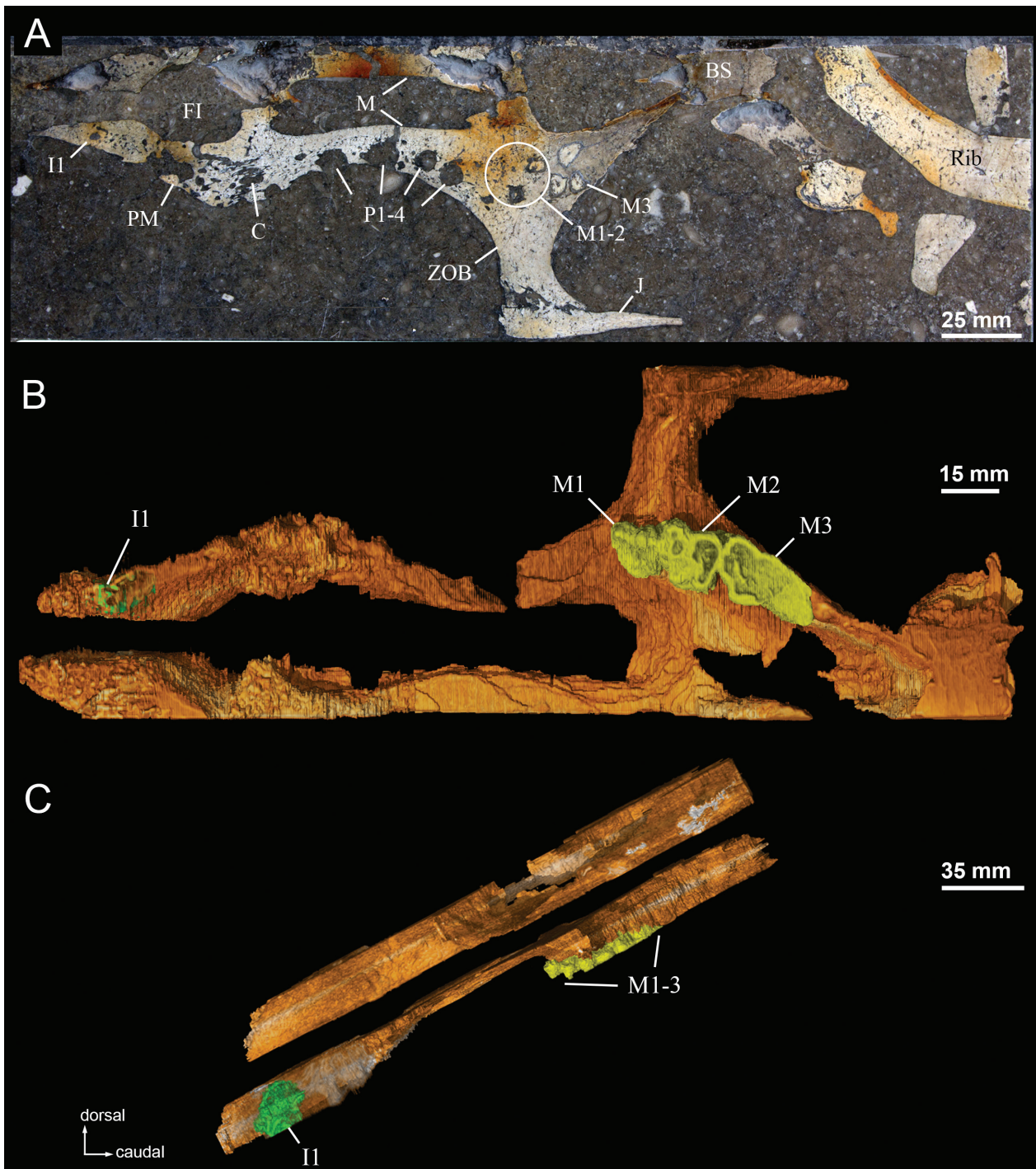
The subsequent new results on the morphology and taxonomy of the Girona specimen include additional data on the premaxilla, the maxilla (zygomatic-orbital bridge), the basicranium, and the dentition. All comparative descriptions rely on the preserved features only.

For the premaxilla, plesiomorphic conditions of the dental formula have been assumed by Voss et al. (2019). However, analyses of the CT-scans do not allow drawing further conclusions on this. While one pair of upper incisor tusks (I<sup>1</sup>) is clearly indicated by distinct alveoli and verified

by both, macroscopic and CT-data (Fig. 5a, b), further alveoli, i.e., for a second and third upper incisor (I<sup>2-3</sup>), cannot be ascertained from the CT-scans. Although the premaxillary dental formula is known to be complete in *P. veronense* and *P. intermedium* and hence would not provide a distinctive feature on species level here, the morphological information of the Girona specimen remains limited in this regard. As such, the available data of the holotype of *P. ausetanum* cannot be complemented assuming that the Girona sea cow is a representative of that species. The same applies to *P. solei* and *P. montserratense*. While *P. solei* shows an incomplete premaxilla that does not reveal informative characters relevant here, the premaxilla of *P. montserratense* is temporarily not accessible, because the holotype specimen is still embedded in sediment.

Further preserved diagnostic features of the premaxilla refer to the length of the alveolus for the first upper incisor





**Figure 5.** *Prototherium* cf. *ausetanum*, MAC GIR-042375. **A.** Photograph showing the dorsal side of slab 2; **B.** Corresponding CT-scan showing the ventral side of slab 2 focusing on the dentition; **C.** CT-scans of anatomically correct combined slab 1 and 2 in lateral view. The CT-scan of the lower side of slab 2 (**B**) reveals the crowns of the upper molars 1–3 ( $M^{1-3}$ ) with the  $M^3$  fully erupted and clearly in wear. Abbreviations: BS, basisphenoid; C, upper canine; FI, foramen incisivum; I1, first upper incisor; J, jugal; M, maxilla;  $M^{1-3}$ , first to third upper molars;  $P^{1-4}$ , first to fourth permanent upper premolars; PM, premaxilla; ZOB, zygomatic-orbital bridge of maxilla.

(I<sup>1</sup>). Slab 2 reveals the alveoli of both I<sup>1</sup> (Fig. 5a, b). While the alveolus on the right side is distorted by inclusions, the one on the left side is already shown to be tapered dorsally indicating the uppermost part of the alveolus (Fig. 5c). Slab 2 represents the lower 2 cm of the preserved partial skull with the left side reflecting a more ventral level than the right side. Hence, it is plausible to conclude that the

left I<sup>1</sup> alveolus definitively did not exceed half the length of the premaxillary symphysis considering slab 1 and the interspace between slab 1 and 2, both commencing at least 3 cm (Fig. 5c). Moreover, it is likely that the I<sup>1</sup> alveolus extends even less than half the length of the symphysis similar to *P. veronense* and *P. intermedium* (re-scored by Voss 2013: character 157), even though it is not exactly

clear how much of the dorsalmost and ventralmost parts of the premaxilla are missing in MAC GIR-042375.

Another morphological feature with diagnostic value is related to the position of the zygomatic-orbital bridge of the maxilla with respect to the palate (e.g., Domning 1994: character 11; Voss 2013: character 21; Springer et al. 2015). According to Balaguer and Alba (2016), it is more or less level with the alveolar plane in *P. ausetanum* (about 6 mm above the tooth arcade). This is also the case with the Girona specimen as can be inferred from the CT-Scan shown in Fig. 4c. In fact, the zygomatic-orbital bridge in MAC GIR-042375 is even on the same level with the tooth arcade. While this condition is also observable in *P. solei*, this is a strong contrast compared to *P. veronense* and, according to personal observations also to *P. intermedium*, where the zygomatic-orbital bridge is elevated above the palate, with its ventral surface lying more than 15 mm above the alveolar margin (Voss 2013). In *P. montserratense*, the zygomatic-orbital bridge is not accessible.

The morphology of the basicranium may have very likely diagnostic value. As stated above, the basisphenoidal-basioccipital region is preserved, which is best visible in macroscopic view of slab 1 (Fig. 4a). Amongst sirenians, the shape of the sphenoccipital eminences varies in either being concave or convex, and therefore, may provide differences at species level (Voss 2013). While these are convex in *P. veronense* and *P. montserratense*, they are concave in *P. intermedium*. This is a similarity with the Girona sea cow MAC GIR-042375. The postulated concavities at this level in macroscopic view are supported by the respective CT-scan (Fig. 4b). In *P. ausetanum*, this character cannot be assessed, because the respective area is incomplete, covered by sediment and deformed insofar that bony material from the right side overlay the posteroventral region of the skull (Jordi Balaguer 2023, pers. comm.). In *P. solei*, the basicranium is not preserved.

At this point also a correction as to the presence of a hypoglossal foramen is made (Voss et al. 2019: fig. 6a). CT-scanning and post-processing do not confirm a hypoglossal foramen on the left side of the basioccipital. Instead, the visible “foramen” in Fig. 4 is either the result of an inclusion or it could be a ventral excavation in the basioccipital, a pharyngeal fossa (PF). However, a hypoglossal foramen, if present in that species, would be positioned more caudad within the basioccipital.

Moreover, our examination of the preserved  $M^{1-3}$  crowns in deeper levels of slab 2 further helps to substantiate the taxonomic identity of the Girona specimen (Fig. 5a). Compared with the species of *Protherium*, it shows differences in the mesiodistal length of the molars (Table 1). The  $M^1$  in MAC GIR-042375 is generally smaller than in the three *Protherium* taxa hitherto considered valid with a deviation of about 16% and 21% in *P. veronense* and *P. intermedium*, respectively, but only 2% in *P. ausetanum* if the  $M^1$  from the left side is compared. The  $M^2$  is also distinctly smaller than in *P. veronense* and *P. intermedium* having a difference of

18% and 9.5%, respectively, but it is about 5% larger than in *P. ausetanum*. With the exception of *P. intermedium*, which lacks respective information (presumably, because both  $M^3$  in the holotype are not fully measurable according to personal observations), the mesiodistal length of the  $M^3$  in the Girona sea cow is 11% and 5% smaller than in *P. veronense* and *P. ausetanum*, respectively.

Extending the comparisons upon the preserved  $M^{2-3}$  in *P. solei* and *P. montserratense* from Spain unveils interesting results. The  $M^{2-3}$  in MAC GIR-042375 (and in *P. ausetanum*) is about 13% and 12% larger than in *P. solei*, respectively, making the latter species the smallest in terms of the molar dimensions. However, compared with *P. montserratense*, the  $M^{2-3}$  are almost as large as in MAC GIR-042375 (Table 1). Taken together, these measurements point to a sirenian that is rather small compared with the *Protherium* taxa from Italy, but that is very similar in size compared with *P. ausetanum* and *P. montserratense* from Spain.

**Table 1.** Mesiodistal length of molars  $M^{1-3}$  of the “Girona specimen” MAC GIR-042375 compared to other *Protherium* species: data for *P. veronense* and *P. intermedium* are taken from Pilleri et al. (1989: table VII), and data for *P. ausetanum* are from Balaguer and Alba (2016: table 2). Measurements for *P. solei* and *P. montserratense* were taken personally and are similar or correspond, respectively, to Pilleri et al. (1989: table on page 19 and table XIII). l and r correspond to measurements from the left and right side, respectively.

	mesiodistal length in mm		
	$M^1$	$M^2$	$M^3$
<i>P. veronense</i> (cast of holotype)	16	21	23
<i>P. intermedium</i> (holotype)	17	19	/
<i>P. ausetanum</i> (holotype)	13.8 l / 15.5 r	16.3 l / 16.6 r	21.6 l / 21.4 r
Girona specimen (MAC GIR-042375)	13.5	17.2	20.5
<i>P. montserratense</i> (holotype)	/	17	21
<i>P. solei</i> (holotype)	/	15	18

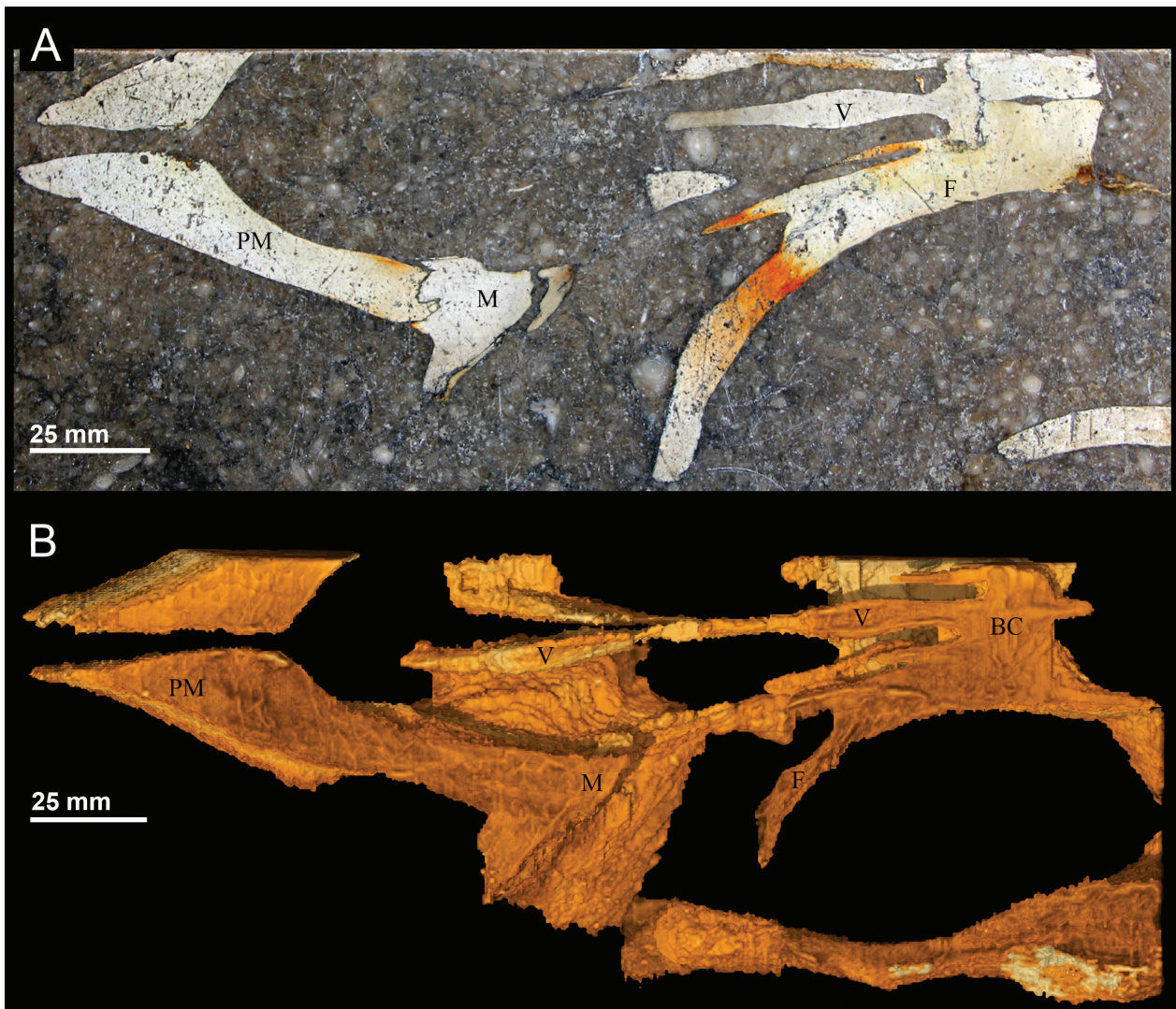
Another molar feature to distinguish MAC GIR-042375 refers to the shape of the  $M^{2-3}$ . Except for *P. ausetanum*, all taxa for comparison show a trapezoid  $M^2$ , with the protoloph each wider than the metaloph, whereas in both, MAC GIR-042375 (Fig. 5b) and *P. ausetanum* (Balaguer and Alba 2016: fig. 4), the proportions of the lophs are similar resulting in a rather rectangular outline of the  $M^2$ . Similarly, the  $M^3$  is trapezoid in all *Protherium* species from Italy and Spain, but not in MAC GIR-042375 (Fig. 5b) and *P. ausetanum* (Balaguer and Alba 2016: fig. 4) where the  $M^3$  is rather oval and tapering distad.

In the following, the description of specimen MAC GIR-042375 is complemented with regard to the preserved morphology visible in slab 1 (Fig. 6) in order to provide overall insights to the reader.

The CT-scan of the slab represents a relatively deep level of the upper part of the skull (Fig. 6b).

After post-processing, the nasal area could be made well visible by reconstructing the extension of the vomer. The vomer is a mediolaterally thin element and triangular





**Figure 6.** *Prototherium* cf. *ausetanum*, MAC GIR-042375. **A.** Photograph; **B.** Corresponding CT-scan of slab 1 providing data on the overall morphology of the specimen. Abbreviations: BC, basicranium; F, frontal; M, maxilla; PM, premaxilla; V, vomer.

in cross section as in other sirenians. It passes through most of the internal narial passage, contacts the maxilla laterally (and most likely the palatine, that, however, cannot be distinguished here) and extends in a longitudinal groove on the dorsal surface of the maxilla slightly forward into the mesorostral fossa (external nasal opening). Anteriorly, the vomer builds up the nasal septum. Posteriorly, the vomer runs indistinctly out into the basicranium.

On the left side, parts of the frontal are visible with the slightly downturned supraorbital process. A complex of remnants of the left jugal anteriorly and the left zygomatic process posteriorly indicate the zygomatic arch of the squamosal.

## Discussion

The analysis of the CT-Scans resulted in a genuine added value in terms of supplemented morphological data that allow for a more coherent taxonomic assignment of the Girona sea cow.

First of all, this specimen is undoubtedly considered as representing a *Prototherium* species. As mentioned above, the key characteristic for the genus *Prototherium* is the lack of a persistent DP<sup>5</sup>/DP<sub>5</sub> (e.g., Domning 1994; Bizzotto 2005; Balaguer and Alba 2016) that is also supported in this study.

Taking into account observations in more derived sea cows, i.e. members of the Dugonginae that show mesial drift of their molars and, as a consequence, lose preceding teeth in lifetime, one can argue that there may have been an unreplaced DP<sup>5</sup> that was worn out and shed given the advanced age of the Girona specimen. The gap between P<sup>4</sup> and M<sup>1</sup> would then have been closed by mesial drift. Although this is an interesting perspective, it is likewise a difficult one. For example, there are two specimens known from Eocene strata representing adults of “*Halitherium*” *taulannense* that show irregular resorption of DP<sup>5</sup>/DP<sub>5</sub> (holotype skull RGHP D040 and paratype mandible RGHP E.7.096a (Voss 2013)). The respective specimens reveal traces of resorption in so far that the area between P<sup>4</sup>/P<sub>4</sub> and M<sup>1</sup>/M<sub>1</sub> is roughened and spongy,

but still retracing the former alveoli. Mesial drift however is not indicated in those specimens.

Traces of resorption are commonly present in specimens that are known to have lost teeth due to mesial drift, especially amongst members of the subfamily Dugonginae that are characterized by the reduction of the antemolar dentition (e.g., Domning 1989). According to Luckett (1993), resorption can take place in different degrees. For example, this is observable in the maxilla of *Dioplotherium manigaulti* Cope, 1883 in which the antemolar area is characterised by bone-filled, degenerated alveoli indicating the former presence of deciduous premolars; the only distinct socket remaining in this roughened area is for the lingual root of the originally three-rooted DP<sup>5</sup> (Domning 1989). Exactly such traces of resorption are missing in the Girona specimen. Instead, the area between P<sup>4</sup> and M<sup>1</sup> appears to be unsuspecting as are the roots of the preserved molars that do not indicate mesial drift (Fig. 5a, b). Consequently, the lack of a persistent DP<sup>5</sup>/DP<sub>5</sub> as a generic distinguishing feature for *Protherium* is not questioned here.

Although the data basis remains limited not at least due to the lack of material between and in each of the two fossil-bearing slabs, the present study provides a combination of characters that argues with the utmost probability for the Girona specimen as being a representative of *P. ausetanum*. Two characters corroborate that hypothesis on the species level and refer to the shape of the M<sup>2</sup> and M<sup>3</sup>. As outlined above, only MAC GIR-042375 and *P. ausetanum* share a rectangular M<sup>2</sup> as well as an oval M<sup>3</sup>. Three further characters that do not argue unambiguously for a taxonomic assignment to *P. ausetanum*, but can be put into perspective, refer to the mesiodistal length of the molar crowns, the position of the zygomatic-orbital bridge, and the shape of the spheno-occipital eminences. Of all taxa for comparison, the mesiodistal length especially of M<sup>2-3</sup> is most similar between MAC GIR-042375, *P. ausetanum*, and *P. montserratense*. A zygomatic-orbital bridge nearly level with the alveolar margin is congruent only in MAC GIR-042375, *P. ausetanum*, and *P. solei*. While *P. montserratense* differs from MAC GIR-042375 in having convex spheno-occipital eminences (a morphological feature that is also present in *P. veronense*), personal observations of the holotype specimen also reveal that it is not fully grown. This is indicated by the non-obiterated spheno-occipital suture and the only slightly worn M<sup>3</sup>. As such, the subadult age may qualify the current results on the mesiodistal length of M<sup>2-3</sup> in *P. montserratense*. The material basis of *P. solei* does not provide further morphological characters that can be compared here. However, three differing dental characters as mentioned above versus one shared cranial character, i.e. the level of the zygomatic-orbital bridge, question a taxonomic assignment of MAC GIR-042375 to *P. solei*. Against that background, the feature of concave spheno-occipital eminences in the Girona specimen may potentially supplement the morphological information of the holotype of *P. ausetanum*, which lacks respective data.

In fact, these eminences are likewise concave in *P. intermedium*, but the latter differs from MAC GIR-042375 in the dental features outlined above and in that the zygomatic-orbital bridge is clearly elevated above the alveolar margin. As such, the fossil sea cow remains from Girona resp. Sant Vicenç de Castellet contribute to more and new information that enhance and supplement our knowledge on the morphology and, considering the similar age and area, distribution of *P. ausetanum*.

In addition to the morphology, the stratigraphy and palaeogeography implicate, at least in part, new hypotheses on the taxonomic identity of the species for comparison, which, conversely, support the assignment of MAC GIR-042375 to *P. ausetanum*. In the Bartonian, potentially four *Protherium* taxa are present in southern Europe: *P. ausetanum* (including MAC GIR-042375), *P. montserratense* and *P. solei*, each from Spain, and *P. veronense* from Italy. For the latter species, different and sometimes contradictory information on its geological age exist throughout the literature, and therefore, this issue shall be clarified first. Apart from Bizzotto (1983: 106) and Balgauer and Alba (2016), for example, who provided a Bartonian age for *P. veronense*, it is also indicated as coming from late Eocene (Priabonian) strata (Domning 1994, 1996; Zalmout and Gingerich 2012: table 1). Meanwhile, the age of the find locality of *P. veronense*, Monte Duello in the Italian Province of Verona, is considered to pertain to the middle Eocene, i.e. Bartonian (Zorzini et al. 2012; Zorzini and Frisone 2013), making this taxon synchronous with the sirenians from Spain. The only *Protherium* species coming from stratigraphically younger sediments, i.e. Priabonian, is *P. intermedium* from Italy (Bizzotto 1983; Domning 1996). Interestingly, the stratigraphically older and palaeogeographically more distant species, *P. montserratense* and *P. solei* (Pilleri et al. 1989), are considered synonymous with *P. intermedium*, either both (Domning 1996) or only *P. solei* (Sagne 2001; Balgauer and Alba 2016). New hypotheses about the validity of the synonymously treated species are discussed as follows.

As outlined above, the present study provides morphological information from the not yet fully prepared holotype of *P. montserratense* that is even now valuable for comparison. For the time being, the morphological characters of it presented here argue for a species distinct from *P. intermedium*, hence, neither supporting a synonymy (Domning 1996: 388) nor the status of a subspecies (Bizzotto 2005) with the latter taxon. While Sagne (2001) already refuted the synonymy of *P. montserratense* with *P. intermedium* on a morphological basis, the distinction of both is also reinforced by their stratigraphic and palaeogeographic data. Moreover, *P. montserratense* is not considered a *nomen dubium* (Balgauer and Alba 2016) though this treatment is well noted as being only provisional pending further investigations. Instead, similarities with *P. veronense* (and differences with *P. intermedium*) like convex spheno-occipital eminences, may argue for the hypothesis that *P. montserratense* is a subadult representative of the



former, hence potentially synonymous with *P. veronense*. Such synonymy that was also pondered by Balaguer and Alba (2016) would be additionally in accordance with the stratigraphic occurrence of both and the consideration of sirenians as migrating species. This hypothesis finds support through a number of other morphological features that are, however, not present in the object of this study. Taking into account that a taxonomic revision of the genus *Prototherium* is not the scope of the present study, this shall nevertheless be shortly outlined here. For example, *P. veronense* and *P. montserratense* show a ventral border of the horizontal mandibular ramus that is tangent to the angle as well as a posterior border of the mandible that has a distinct steplike process below the condyle, both character states contrasting with *P. intermedium* (Voss 2013: appendix 4). Therefore, it shall be emphasized here that it is highly relevant to examine the holotype specimen of *P. montserratense* completely in order to clarify its status, either as a distinct, and hence valid species, or a synonym of *P. veronense*.

Similarly, *P. solei* is questioned here to be either a junior synonym (Domning 1996; Sagne 2001; Balaguer and Alba 2016) or a subspecies (Bizzotto 2005) of *P. intermedium*. On the one hand, the stratigraphic and palaeogeographic data provide arguments for a distinction of both species. On the other hand, morphological differences like the position of the zygomatic orbital bridge argue against an assignment of *P. solei* to *P. intermedium*. Considering again characters beyond those preserved in the object of this study, the mandibular morphology in *P. solei* reveals an interesting combination of characters. The course of the ventral border of the horizontal ramus that is most likely tangent with the angle resembles that in *P. montserratense* and *P. veronense*, whereas the posterior border of the mandible seems to lack a distinct process below the condyle similar to *P. intermedium*. In summary, *P. solei* demonstrates similarities and, at the same time, differences with all taxa for comparison, including *P. ausetanum* (and MAC GIR-042375). These incongruences illustrate that *P. solei* needs to be carefully reinvestigated in consideration of the other *Prototherium* species aiming at a thorough revision of the genus in total. As such, and for the time being, *P. solei* is provisionally treated as a distinct species according to Pilleri et al (1989).

Further studies could also help to fix the issue of the controversially discussed interrelationships of the genus *Prototherium*, which is shown as para- and polyphyletic in Balaguer and Alba (2016) as well as in the first (Domning 1994) and the most recent (Díaz-Berenguer et al. 2022; Heritage and Seiffert 2022) cladistic analyses of sirenians. In Vélez-Juarbe and Wood (2018), the interrelationships of Eocene sirenians, including *Prototherium*, are not resolved at all, showing a large polytomy. Domning (1996: 388) already assumed that *P. intermedium* is probably generically distinct from *P. veronense*, a hypothesis that has not further developed until to date. Therefore, this issue should be rather addressed after a thorough taxonomic-morphological revision of the genus,

including the clarification of the status and affinities of *P. solei* and *P. montserratense* as outlined above.

This approach is particularly suggested in light of an alternative phylogenetic hypothesis that supports the monophyly of *Prototherium* by showing a sister group relationship between *P. veronense* and *P. intermedium* (Voss 2013). This sister grouping is confirmed by a unique combination of homoplasies and a good agreement between the phylogeny and stratigraphy (Voss 2013: fig. 75). Except character 21 referring to the level of the zygomatic-orbital bridge (Voss 2013), none of the features supporting the sister grouping are preserved in MAC GIR-042375. Therefore, Voss' (2013) data set and cladistic analysis shall be updated and tested for stability first before further conclusions on the phylogenetic interrelationships are drawn.

Considering the bigger picture, better-resolved intra- and intergeneric relationships based on new informative fossils such as MAC GIR-042375 have the potential to contribute to a better understanding of the interrelationships of Eocene taxa and sirenians in total. Although this task is beyond the scope of this paper, it shall be outlined here that the classification of Sirenia has long been controversial. In other words: the traditional classification concept of Sirenia, which distinguishes four families (e.g., Domning 1996), is incongruent with the results of phylogenetic analyses of the order. This refers especially to the Dugongidae, the family that *P. ausetanum* is traditionally referred to according to Balaguer and Alba (2016). While only two dugongid groups are consistently revealed as monophyletic, the derived Dugonginae and Hydrodamalinae, Eocene dugongids are conspicuously paraphyletic as well as most of the genera (e.g., Domning 1994; Springer et al. 2015). Additionally, some approaches (e.g. Vélez-Juarbe et al. 2012; Springer et al. 2015) reveal Dugongidae as a clade, whereas other studies, including one of the latest (Domning 1994; Voss 2013; Díaz-Berenguer et al. 2018), do not affirm this hypothesis. Consequently, Eocene sirenians, and Eocene dugongids from the traditional point of view, represent one of the most controversially discussed taxa.

In order to solve this drastic paraphyly problem, Voss (2013) proposed the total group concept (Jefferies 1979) and distinguishes a stem group, which, by definition, is consistently paraphyletic, and a monophyletic crown group within the clade Sirenia, hence setting aside the traditional classification concept of four sirenian families. In the same year, and as already outlined in the Systematic palaeontology chapter, O'Leary et al. (2013) introduced Pan-Sirenia as the most inclusive group comprising all species more closely related to crown-Sirenia than to any other living species. This finds also consideration in the very latest and total evidence phylogenetic analysis by Heritage and Seiffert (2022). As such, Eocene dugongids in the traditional sense (compare previous studies cited above) fall into the stem group of Pan-Sirenia. Most of the more derived dugongids are part of crown-Sirenia and form the more exclusive, but monophyletic Dugongidae

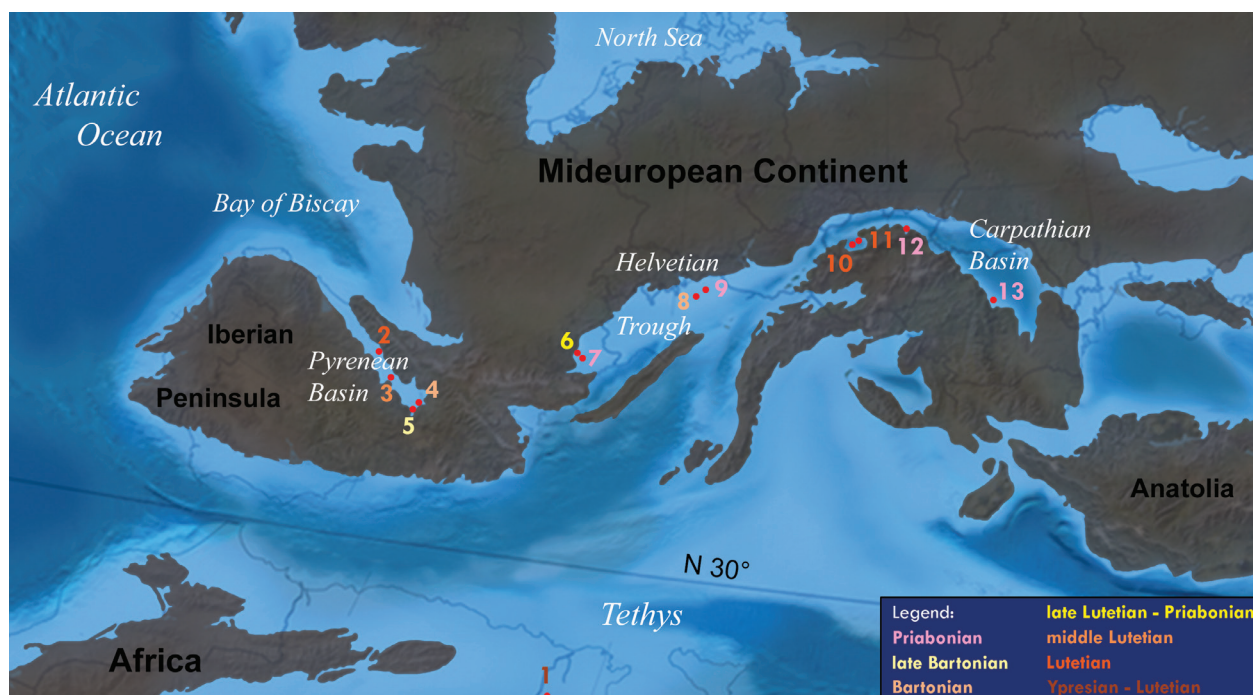
as defined by Heritage and Seiffert (2022). In terms of *P. ausetanum*, this species has to be considered now as a stem-group representative, i.e., a pan-sirenian that falls outside crown-Sirenia.

## Palaeobiogeographic overview

Fig. 7 shows a comprehensive selection of Eocene pan-sirenian findings from Central and South Europe, and North Africa, providing an overview on the distribution of that group in this region and time frame.

There is a rough SW-NE direction or tendency of distribution regarding the geological ages of the records. In the southwestern Tethyan area, ear bones from the early Eocene (Ypresian) of Tunisia represent the oldest sea cow remains (Benoit et al. 2013). Although the taxonomic identity of these periotics remains unclear, the morphology of these is even more primitive compared to those from the hitherto earliest known prorastomids (*Prorastomus* and *Pezosiren*), and pan-sirenians at all, from Jamaica (Benoit et al. 2013). There are also stratigraphically old pan-sirenians known from the early middle Eocene (Lutetian) of the Pyrenean Basin with taxonomically not further defined postcrania

from Navarre (late Lutetian of Spain; Astibia et al. 2010) as well as the recently established and even older species *Sobrarbesiren cardieli* from Huesca (middle Lutetian of northeastern Spain; Díaz-Berenguer et al. 2018). The latter is especially interesting since it represents the first adequately known quadrupedal sea cow from Eurasia, including several skulls and diverse postcranial elements (Díaz-Berenguer et al. 2020). In the deepest embayment of the Pyrenean Basin, *P. ausetanum* is documented from younger middle Eocene sediments, i.e., Bartonian. This refers to the likely representative from Girona described by Voss et al. (2019) and reviewed herein, and the holotype specimen from Tona (Balaguer and Alba 2016). These records are followed up northeastwards by on trend younger fossils such as several skulls, mandibles and postcranial material of *Eotheroides* sp. (late Lutetian to Priabonian) and “*Halitherium*” *taulannense* (Priabonian), both from Taulanne (Alpes-de-Haute-Provence, France; Domning et al. 1982; Sagne 2001), and the Bartonian *P. veronense* (de Zigno 1875) and the Priabonian *P. intermedium* (Bizzotto 1983), both from within the Helvetian trough of North Italy. The known pan-sirenian fossils from the Eocene of Hungary still show a stratigraphic range. While the partial skull and mandibular fragment of *Sirenavus hungaricus* (Kretzoi 1941) as well



**Figure 7.** Palaeogeographic map of Europe during the Eocene based on templates of Ron Blakey (2020) showing relevant sirenian findings. **1**, Pan-Sirenia indet., Ypresian-Lutetian of Jebel Chambi, Tunisia (Benoit et al. 2013); **2**, ?Dugongidae indet. (according to the traditional classification concept – but most likely Pan-Sirenia indet.), Lutetian of Navarre, Western Pyrenees, Spain (Astibia et al. 2010); **3**, *Sobrarbesiren cardieli*, middle Lutetian of Castejón de Sobrarbe, Huesca, Spain (Díaz-Berenguer et al. 2018); **4**, *Protheroherium ausetanum*, Bartonian of Tona, Catalonia, Spain (Balaguer and Alba 2016); **5**, *Protheroherium* cf. *ausetanum*, late Bartonian of Sant Vicenç de Castellet, Catalonia, Spain (this paper); **6**, *Eotheroides* sp., late Lutetian-Priabonian of Taulanne, Alpes-de-Haute-Provence, France (Domning et al. 1982); **7**, “*Halitherium*” *taulannense*, Priabonian of Catellane, Alpes-de-Haute-Provence, France (Sagne 2001); **8**, *Protheroherium veronense*, Bartonian of Monte Duello, N Italy (De Zigno, 1875); **9**, *Protheroherium intermedium*, Priabonian of Possagno, N Italy (Bizzotto 1983); **10**, *Sirenavus hungaricus*, Lutetian of Felsögalla, Hungary (Kretzoi 1941); **11**, *Anisotirenian pannonica*, Lutetian of Oroszlány, Hungary (Kordos 1979); **12**, *Paralitherium tarkanyense*, Priabonian of Felsőtarkány, Hungary (Kordos 1977); **13**, Sirenia indet. (most likely Pan-Sirenia, see Discussion), Priabonian of Cluj-Napoca, Romania (Fuchs 1970).



as the maxilla of *Anisosiren pannonica* (Kordos 1979) are recorded from the Lutetian, the mandibles of *Paralitherium tarkanyense* (Kordos 1977) are Priabonian in age. Apart from that, a single cranial roof documents a Priabonian occurrence in the northeast-most European Tethyan realm of the Carpathian Basin and is determined as Sirenia indet. from Romania (Fuchs 1970).

In light of this stratigraphic and taxonomic background, the hypothesis on a Tethyan origin of sea cows is reinforced. Pan-Sirenia form a well-substantiated clade called Tethytheria together with their extant sister group Proboscidea (McKenna 1975; McKenna and Bell 1997). While the origin of the latter is well-recorded in Africa, the earliest pan-sirenians have long been only known from the Eocene of Jamaica (Savage et al. 1994; Domning 2001a, b). The periotics from the late Ypresian-early Lutetian (late early-early middle Eocene) of Tunisia do not only represent the oldest sea cow remains from Africa (Benoit et al. 2013), but can be now also considered to predate *Prorastomus sirenooides* from Jamaica according to Heritage and Seiffert (2022). Additionally, the morphology of the ear bones reflects more plesiomorphic conditions than those of *P. sirenooides* (Benoit et al. 2013), which is also shown by Heritage and Seiffert (2022), who phylogenetically identify the Tunisian find as the basal-most pan-sirenian. Thus, the morphological, stratigraphic and biogeographic evidence corroborates a North African origin of Pan-Sirenia that, in turn, contributes to a better understanding of the Tethytheria hypothesis (e.g., Tassy and Shoshani 1988; Murphy et al. 2001).

Although a fast dispersal remains a solid hypothesis in the evolutionary history of stem pan-sirenians (e.g., Domning 1994), this no longer includes the Jamaican prorastomids alone, but also a number of European fossils and taxa from the early middle Eocene (Lutetian) as mentioned above. Especially the Pyrenean Basin appears to be a kind of hot spot that yielded a number of stem sea cows limited to the middle Eocene. On the one hand, *Sobrabesiren cardieli* is the hitherto oldest record of western Europe and the only quadrupedal form of Eurasia (Díaz-Berenguer et al. 2018), hence providing one of the rare examples for dispersal amongst early pan-sirenians that probably had an already fully aquatic lifestyle (Díaz-Berenguer et al. 2020: 672). On the other hand, the Bartonian *P. ausetanum* including the Girona specimen (Balaguer and Alba 2016; Voss et al. 2019) indicates further diversification in this area. With emphasis on the North African – Eurasian Tethyan realm considered here (Fig. 7), the southwestern Tethys is hypothesized as the evolutionary center for Eocene Pan-Sirenia, from where they dispersed westwards through the Atlantic (Benoit et al. 2013; Heritage and Seiffert 2022) as well as northwards through the Tethyan Ocean.

## Conclusions

The present study incorporates the non-invasive analysis of CT-scans and macroscopic data generated from

a sirenian find embedded in two paving slabs. On the basis of these data, and supplementing the results from Voss et al. (2019), the Girona sea cow MAC GIR-042375 belongs to the genus *Prototherium* and most likely represents *P. ausetanum* Balaguer & Alba, 2016 from the middle Eocene of Catalonia (Spain). Morphological results on the maxilla, the basicranium, and the dentition confirm and complement the available information of the holotype of that species. Against the background that MAC GIR-042375 is determined as adult, it is especially the mesiodistal length of the molar crowns that outline *P. ausetanum* as a small-sized species in general, hence distinct from other *Prototherium* taxa.

Considering the distribution of stem pan-sirenians across Eurasia in total, the records not only reflect a rough southwest-northeast oriented trend towards younger geological ages, but also mark the Pyrenean Basin as one of the centers of abundant and well-preserved pan-sirenians, including nearly complete skulls and skeletons even of a plesiomorphic evolutionary stage like *Sobrabesiren cardieli* (Díaz-Berenguer et al. 2018).

## Data availability

The paving stones containing the fossil sea cow remains are being exhibited in the Museu d'Arqueologia de Catalunya (Archaeology Museum) in Girona and have the collection number MAC GIR-042375.

All CT images of this sirenian are archived in the Museum für Naturkunde and accessible through the Department of Science Data Management under <https://doi.org/10.7479/c65w-cj22> (Voss et al. 2022; Cranial CT-data of Eocene *Prototherium ausetanum* from Catalonia compared to a *Dugong* skull [Dataset], shared under a Creative Commons CC-BY license).

## Author contribution

MV and OH conceived the research, processed the morphological analyses and wrote the manuscript. JCV run the CT analyses at the Clínica Girona. KM finalised segmentation of the CT data and provided the 3D reconstruction. MV prepared Figs 3 to 6. OH produced Figs 1, 2 and 7. All authors edited the final version of the manuscript.

## Competing interest

The authors declare that they have no conflict of interest.

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